J. HYM. RES.
Vol. 19(1), 2010, pp. 77–83

Plega hagenella (Neuroptera: Mantispidae) Parasitism of *Hylaeus (Hylaeopsis)* sp. (Hymenoptera: Colletidae) Reusing Nests of *Trypoxylon manni* (Hymenoptera: Crabronidae) in Trinidad

Allan W. Hook, John D. Oswald, and John L. Neff

(AWH) Department of Biological Sciences, St Edward's University, Austin, TX 78704-6489, USA; allanh@stedwards.edu
(JDO) Department of Entomology, Texas A&M University, College Station, TX 77845-2475, USA
(JLN) Central Texas Melittological Institute, 7307 Running Rope, Austin, TX 78731, USA

Abstract.—Two adult specimens of *Plega hagenella* were reared from a nest of the crabronid wasp *Trypoxylon manni* collected in Trinidad in 2008. The mantispids developed by feeding on the immature stages of a colletid bee, *Hylaeus (Hylaeopsis)* sp., which had secondarily occupied the cells of the aerial mud nest of *T. manni*. Two dead *Hylaeus* pupae were found within the nest, one of which had six dead mantispid larvae attached. Numerous insect egg chorions, interpreted as belonging to *P. hagenella*, were found in clusters inserted into small cavities in the mud of the outer surface of the nest. Five additional adult *P. hagenella* were collected in microhabitats where other *T. manni* nests were collected. These new observations confirm the presence of *P. hagenella* in Trinidad, establish the presence of the subgenus *Hylaeopsis* in Trinidad, and document *Plega hagenella* as a new parasite of bees in the genus *Hylaeus*.

The insect order Neuroptera – lacewings, antlions and their relatives – currently comprises approximately 5,730 valid extant species placed in about 17 families. The family Mantispidae – mantispids or mantis-flies – form a distinctive clade of about 395 species that is well known for the raptorial forelegs of its predatory adults, and the larval life history strategy of species in the subfamily Mantispinae as spider egg parasites. Less well known are the larval strategies of species in the three other extant mantispid subfamilies – the Symphrasinae, Drepanicinae and Calomantispinae – none of which are known to be associated with spiders.

Of particular interest are larval associations of species belonging to the subfamily Symphrasinae, which is generally considered to be the sister-group to all other mantispid subfamilies collectively (Penny and da Costa 1983; Lambkin 1986). The biologies of symphrasine species are poorly known and, consequently, new host records are of considerable interest. The Symphrasinae contains three extant genera – *Anchieta*, *Trichoscelia* and *Plega* – all of which are currently restricted to the New World (Penny 1982), and for each of which few larval host/feeding records are available. *Anchieta* includes five species known from Brazil and French Guiana, only one of which has a reported host: *A. fumosella* (Westwood), which has recently been reared from cocoons of *Trypoxylon* (*Trypargilum*) *aestival* Richards in southeastern Brazil (Buys 2008). *Trichoscelia* contains 13 species distributed from southern Mexico south to Uruguay, Argentina and southern Brazil (Penny 1982; Ohl 2004). *Trichoscelia varia* (Walker) has been reared from nests of the vespid wasps, *Polybia ruficeps* Schrottky and *P. scutellaris* (White) (Penny 1982); and Dejean and Canard (1990) provide an interesting account of *Trichoscelia santareni* (Navás) invading a colony of *Polybia diguetana* Buysson on the Yucatan Peninsula.

Table 1. *Plega melitomae* species-group host records.

Plega sp.	Host record	Location	Reference
beardi(?)	*Trypoxylon albitarse* (Crabronidae)	Trinidad	Penny 1982
hagenella	*Hylaeus (Hylaeopsis)* sp. (Colletidae), in *Trypoxylon manni* nest	Trinidad	(this work)
melitomae	*Melitoma segmentaria* (as *M. euglossoides*) (Apidae)	Mexico (Chiapas)	Linsley and MacSwain 1955
sp. near *melitomae*	*Trypoxylon* sp.	Mexico (Veracruz)	Parker and Stange 1965
yucatanae	*Megachile exaltata* (Megachilidae)	Mexico (Yucatan)	Parker and Stange 1965

Plega includes 14 species distributed from the southwestern United States, south to Bolivia and Brazil (Penny 1982). Two species groups are generally recognized – the *melitomae* and *signata* groups. Members of the *P. melitomae* group (*P. beardi, hagenella, melitomae, paraense* and *yucatanae;* see Penny 1982) have been reported as parasites of several bees and aculeate wasps (Table 1). In contrast to the hymenopteran feeding records of the *melitomae* group, members of the *signata* group have been reared from subterranean insects (Parker and Stange 1965). *Plega signata* Hagen cocoons have been found inside subterranean cocoons of the noctuid moth *Egira curialis* (Grote) (Woglum 1935; as *Xylomyges curialis*). Werner and Butler (1965) presented circumstantial evidence of *Plega banksi* Rehn devouring a scarab pupa as well as an asilid pupa associated with a scarab pupa in Arizona. They suggested that the larvae live in soil as predators.

The global crabronid genus *Trypoxylon,* which figures prominently in several host records for the *P. melitomae* group, contains more than 600 species and is well represented in the New World. *Trypoxylon manni* Richards is known from Brazil and Trinidad and commonly attaches its nests to rootlets under dirt banks next to road cuts in the Northern Range, Trinidad, West Indies (Vesey-FitzGerald 1936). Nests of *T. manni* are often communal and may contain up to six females and 64 cells (Hook and Starr unpubl.). *Trypoxylon manni* is a member of the *T. fabricator* group, in which nest sharing by females is known in at least three species: *T. fabricator* Smith (Sakagami et al. 1990), *T. maidli* Richards and *T. manni* (Hook and Starr pers. obs.).

MATERIALS

Between 2003 and 2008 the senior author field collected five specimens of *Plega hagenella* in several places on the island of Trinidad. Three of the specimens were collected in 2008 under dirt banks harboring *Trypoxylon manni* nests. One female was taken on 18 July along the Paria Trail, another female was collected on 23 July up the Maracas Valley in the Northern Range and a male was taken on 25 July in the Arena Forest Reserve. A fourth specimen (male) was collected on 26 July 2003 up the Caura Valley (Northern Range) and a fifth specimen (female) was collected on 25 August 2005 at U.W.I. Flats (apartments) in St. Augustine (*Trypoxylon* spp. were observed nesting around the apartments).

In July of 2008 AWH collected 10 nests of *Trypoxylon manni* – seven from along the upper reaches of the Paria Trail (10.746°N 61.285°W; connecting the village of Brasso Seco to Paria Bay on the north coast) on 18 July, two in the Maracas Valley (10.705°N 61.368°W) on 23 July and one on 25 July along a road entering the Arena Forest Reserve (10.562°N 61.256°W). All nests were collected into and maintained isolated in separate plastic bags in order to rear their contents. Two adults of *Plega* *hagenella*, and numerous presumed eggs and larvae of the same species, were later found to be associated with one of the nests collected along the Paria Trail (AWH field note 36-2008). Most of the cells of this nest were subsequently dissected and examined for evidence of insect occupation and usage. Observations made during the examination of this nest are summarized below.

RESULTS

Observations on Trypoxylon and Hylaeus.—The mantispid-parasitized nest had 14 cells, of which nine were open when collected, two were closed with mud and three were closed with a tough, transparent, membrane indicative of cell reutilization by a colletid bee, subsequently identified as *Hylaeus (Hylaeopsis)* sp. Of nine cells opened by dissection, *Hylaeus* had reutilized eight, as evidenced by typical *Hylaeus*-type transparent cell linings and partitions found within the original mud cells of the *Trypoxylon manni* nest. *Hylaeus* reused 11 of the 14 cells this nest contained. *Trypoxylon* species do not line their nest cells with secretions, but this is a characteristic feature of colletid bee cells (Almeida 2008). Two dead *Hylaeus* pupae were found in these lined exterior cells. Of these, one pupa was unparasitized but the other had six dead mantispid larvae attached to its thorax and abdomen (the head was missing).

Identification of the bee species as *Hylaeus (Hylaeopsis)* sp. is based on the dead pupae found in the nest and on bee rearings from 46 additional *Trypoxylon manni* nests collected previously in 1996 and 1999 (primarily along the Blanchisseuse Road in the Northern Range of Trinidad). Interestingly, a diversity of cleptoparasites was reared from 19 of the earlier 46 nests, but no mantispids. Six (13%) of the 46 nests collected during this earlier period had some level of *Hylaeus* cell reutilization. Those six nests contained a total of 93 cells, of which 16 (17%) were reused by *Hylaeus*, with one to two or possibly three *Hylaeus* cells per *T. manni* cell.

Observations on Plega.—Two adult *Plega hagenella*, one male and one female, were subsequently found in the plastic bag containing the parasitized *Trypoxylon* nest, which had been maintained indoors, dry, and at ambient room temperatures since its collection. The male was discovered nearly dead on 26 July 2008. The nest was subsequently checked irregularly until 18 August. The next inspection was not until 9 October, when a dead female was discovered. The adult *Plega hagenella* specimens were identified using the keys and descriptions of Penny (1982), who noted the existence of previously-collected females resembling, but not conclusively identifiable as, *P. hagenella* from Trinidad. The present material confirms the presence *P. hagenella* in Trinidad based on definitively identifiable male specimens and associated females.

Subsequent examination of the nest revealed two mantispid pupal exuviae, one protruding from each of two nest cells, both of which were marked by the characteristic cellophane-like lining of *Hylaeus*. A loose double-walled cocoon of typical neuropteran form was extracted from one of these cells. In another cell, six neuropteran larvae of at least two sizes were found attached to a dead *Hylaeus* pupa.

Further inspection of the partially dissected nest revealed the existence of numerous, small, whitish, insect egg chorions associated with its outer layers. While some of the eggs may have been deposited on the exposed outer surface of the nest, most appear to have been inserted into small cavities in the nest's irregular mud surface, often in small groups of 3–6 per cavity. The small cavities are natural features of the original mud nest, the result of incomplete joining or smoothing of adjacent, rounded, mud boluses used in its construction. At least 29 empty egg chorions were found in or on the nest, but it seems likely that additional eggs were lost during the dissection of the nest, or were inserted so deeply into crevices that they were hidden from view. The eggs were narrowly lacrimiform in shape (with the micropylar process terminating the narrowed end), ca. 0.7 mm long, simple (i.e., stalkless), and marked externally with a network of raised polygonal ridges. All of the eggs appeared to be empty, their larvae having emerged through longitudinal slits located near the micropylar ends of each egg.

DISCUSSION

Hylaeus (Hylaeopsis).—This Neotropical subgenus of 15 species has been reported from Mexico south to Paraguay and southern Brazil, but it has not previously been reported from Trinidad, the neighboring Guyanas, or Venezuela (Urban and Moure 2007). Ten or more undescribed *Hylaeopsis* species are suspected to be present in the Neotropical fauna (Michener 2007). Adults of the Trinidad *Hylaeopsis* are much smaller than adult *Plega hagenella*, suggesting that *Plega* larvae must consume multiple bee larvae and/or pupae to reach adulthood. If this is true, the pattern of multiple bee cells per wasp cell and gregarious nesting (also reported in *H. (Hylaeopsis) tricolor* (Schrottky) by Sakagami and Zucchi 1978) may contribute to making this bee species a suitable host for *Plega hagenella*. Not all *Hylaeopsis* species nest gregariously, however, and the hyperdispersed, single-celled nests of *H. (Hylaeopsis) grossus* (Cresson) (Michener and Brooks 2003) may be adaptive in helping to avoid attacks by larger nest parasites like *Plega*.

Plega.—Although definitive, reared, larvae and eggs of *P. hagenella* have yet to be described, detailed observations derived from the parasitized *Trypoxylon* nest reported here, together with existing knowledge of mantispid immatures, present a strong circumstantial case that the eggs and larvae noted above are those of *P. hagenella*. The rearing of definitively identified *P. hagenella* adults from the *Trypoxylon* nest renders plausible the discovery of immature *P. hagenella* stages in the same nest. The general morphology of the recovered larvae is consistent with their determination as first-instar mantispid larvae. The larvae are morphologically similar to the first-instar larvae of both *Plega yucatanae* (described by Parker and Stange 1965) and other described first-instar mantispids (e.g., *Climaciella brunnea* [as *Mantispa brunnea*], *Dicromantispa interrupta* [as *Mantispa interrupta*], *Dicromantispa sayi* [as *Mantispa sayi*], *Leptomantispa pulchella* [as *Mantispa pulchella*] and *Zeugomantispa virescens* [as *Mantispa viridis*], see Hoffman and Brushwein 1992; *Tuberonotha strenua* [as *Climaciella magna*] and *Mantispa japonica*, see Kuroko 1961).

The eggs noted above, in addition to being physically associated with the mantispid-parasitized nest, are also consistent both morphologically and behaviorally with a mantispid identification. Their size is appropriate to that of the smaller mantispid larvae observed in the nest. The deep insertion of many of the eggs into fine crevices in the mud surface of the nest is consistent with oviposition via a slender, elongate, ovipositor, the presence of which is, within the order Neuroptera, a synapomorphy of the mantispid subfamily Symphrasinae, to which *Plega hagenella* belongs. Although at least two *Plega* species have been reared from egg to adult (*P. dactylota* and *P. signata*; see MacLeod and Redborg 1982), no published descriptions or illustrations of Symphrasine mantispid eggs exist. Interestingly, however, the eggs noted here bear a strong resemblance to, though are somewhat more slender and elongate than, those illustrated by Minter (1990, fig. 1) for *Mucroberotha vesicaria* – a species belonging to a group of several genera of uncertain phylogenetic placement that have in recent years been placed in either the family Mantispidae or Berothidae (as Rhachiberothinae), or as a separate family (as Rhachiberothidae). The presence of sessile eggs in both rhachiberothines/ids and symphrasine mantispids has potentially interesting implications for the interpretation of the stalked eggs found in both mantispine mantispids and berothine berothids (both of which are relatively derived subfamilies within their families). If sessile eggs are found to be symplesiomorphic in rhachiberothines/ids and symphrasine mantispids, the stalked eggs found in berothines and mantispines are likely to be independent, derived innovations.

Parasite Biology.—Because the *Plega hagenella* adults emerged from the mud nest of *Trypoxylon manni*, it was initially assumed that *P. hagenella* was a parasite of *T. manni*. However, several observations and lines of evidence suggest that, at least in this case, *P. hagenella* was parasitizing the *Hylaeus* (*Hylaeopsis*) sp., not *T. manni*. First, no remnants of *Trypoxylon* immatures were found in the nest, suggesting that the original nest builders had vacated the nest prior to its occupation by *Hylaeus* and *Plega*. Second, all evidence of *P. hagenella* cell occupation (i.e., pupal exuviae, cocoon, presumed larvae) was found in nest cells with membranous linings, indicating an association with the cells reused by *Hylaeus*, rather than the uncoated cells of *Trypoxylon*. Third, the presumed larvae of *P. hagenella* were clearly found in association with a *Hylaeus* pupa in the nest. Several of the larvae appeared to have their jaws successfully inserted into the cuticle of the bee pupa, and differences in the sizes of some of the larvae suggest that at least some had fed successfully. What actually killed the discovered bee pupae and mantispid larvae is unknown. Finally, a bee host for *P. hagenella* is consistent with the known bee hosts of at least two other members of the *Plega melitomae* species group (*P. melitomae* and *yucatanae*; see Table 1). In fact, the three-species interaction documented here – *Plega hagenella* parasitizing a *Hylaeus (Hylaeopsis)* species reutilizing a *Trypoxylon manni* nest – calls into question the accuracy of previous host records of *Trypoxylon* species for other *P. melitomae* group species (Table 1). The discovery of a mantispid-parasitized bee in a reutilized aculeate wasp nest makes it apparent that accurate host records for *P. melitomae* group mantispids cannot be inferred from published associations unless the possibility of nest reuse is explicitly addressed.

The observation that *P. hagenella* adults can be collected in sheltered, exposed-soil, situations favorable for *Trypoxylon* nesting provides a new focal point for field collecting *Plega* adults, which are rather rarely collected in tropical regions. It remains to be determined, however, whether these *Plega* individuals are preferentially targeting bees reusing *Trypoxylon* nests in such microhabitats, or whether they are attracted to such areas for general shelter and/or for access to a potentially larger array of subterranean-, surface- and aerial-nesting aculeate Hymenoptera that would likely be attracted to the same sites because of their suitability for nest-building.

Because of the paucity of available host records, the degree of host-specificity of individual *Plega* species is currently unclear, though the possible division of wild hosts proposed by Parker & Stange (1965) – i.e., *P. melitomae* group species on aculeate Hymenoptera and *P. signata* group species on a larger array of subterranean insects (e.g., larvae and/or pupae of Coleoptera, Lepidoptera and Diptera) – still appears as a broad generalization. It should be noted, however, that this generalization may not apply to captive individuals reared under artificial conditions (MacLeod and Redborg 1982).

All Mantispinae with known biologies have spider-associated larvae, and adults with highly r-selected reproductive strategies, each female producing hundreds to thousands of minute, stalked, eggs that are deposited in the environment with apparently little or no attempt to oviposit in sites that might increase the probability of emerging larvae encountering suitable hosts. The finding of *Plega hagenella* eggs directly deposited on a nest containing the immature stages of its host suggests that *P. hagenella*, and possibly other symphrasine mantispids, employs a different, more targeted, oviposition strategy that actively places eggs in closer proximity to potential hosts. Strategies such as this suggest the existence of more complex adult behaviors, particularly higher levels of host-searching ability in females. Within the Mantispidae, extraordinary intraspecific and oviposition behaviors are also found in the symphrasine species *Trichoscelia santareni*, whose males and females engage in lekking behavior, followed by the females flying to, entering and ovipositing within active vespid nests (Dejean and Canard 1990).

ACKNOWLEDGMENTS

This paper is dedicated to the memory of Roy Snelling. Chris Starr and Carl Fitz-James graciously made their homes available during my stay in Trinidad, and the Department of Life Sciences, The University of the West Indies provided office and laboratory facilities. The Wildlife Section of the Forestry Division, St. Joseph, Trinidad issued collecting and export permits. Voucher specimens are deposited in the University of Texas and Texas A&M University insect collections.

LITERATURE CITED

Almeida, E. A. B. 2008. Colletidae nesting biology (Hymenoptera: Apoidea). *Apidologie* 39: 16–29.

Buys, S. C. 2008. Observations on the biology of *Anchieta fumosella* (Westwood 1867) (Neuroptera: Mantispidae) from Brazil. *Tropical Zoology* 21: 91–95.

Dejean, A. and M. Canard. 1990. Reproductive behavior of *Trichoscelia santareni* (Navás) (Neuroptera: Mantispidae) and parasitism of the colonies of *Polybia diguetana* R. du Buysson (Hymenoptera: Vespidae). *Neuroptera International* 6: 19–26.

Hoffman, K. M. and J. R. Brushwein. 1992. Descriptions of the larvae and pupae of some North American Mantispinae (Neuroptera: Mantispidae) and development of a system of larval chaetotaxy for Neuroptera. *Transactions of the American Entomological Society* 118: 159–196.

Kuroko, H. 1961. On the eggs and first-instar larvae of two species of Mantispidae. *Esakia. Occasional Papers of the Hikosan Biological Laboratory* 3: 25–32.

Lambkin, K. J. 1986. A revision of the Australian Mantispidae (Insecta: Neuroptera) with a contribution to the classification of the family. I. General and Drepanicinae. *Australian Journal of Zoology, Supplementary Series* 116: 1–142.

Linsley, E. G. and J. W. MacSwain. 1955. Two new species of *Plega* from Mexico. *Pan-Pacific Entomologist* 31: 15–19.

MacLeod, E. G. and K. E. Redborg. 1982. Larval Platymantispine mantispids (Neuroptera: Planipennia): possibly a subfamily of generalist predators. *Neuroptera International* 2: 37–41.

Michener, C. D. 2007. *Bees of the World*. Johns Hopkins University Press, Baltimore. xvi + 557 pp.

——— and R. W. Brooks. 2003. Dispersal of brood cells in a Mesoamerican hylaeine bee: a probable risk-spreading behavior (Hymenoptera, Colletidae). Pp. 151–152 *in:* Melo, G. A. R., and I. A. dos Santos eds. *Apoidea Neotropica: homenagem aos 90 anos de Jesus Santiago Moure*. Editora UNESC, Criucuma, Brazil.

Minter, L. R. 1990. A comparison of the eggs and first-instar larvae of *Mucroberotha vesicaria* Tjeder with those of other species in the families Berothidae and Mantispidae (Insecta: Neuroptera). Pp. 115–129 *in:* Mansell, M. W. and H. Aspöck eds. *Advances in Neuropterology. Proceedings of the Third International Symposium on Neuropterology* (3–4 February 1988, Berg en Dal, Kruger National Park, South Africa). South African Department of Agricultural Development, Pretoria. 298 pp.

Ohl, M. 2004. Annotated catalog of the Mantispidae of the World (Neuroptera). *Contributions on Entomology, International*. 5: 131–262.

Parker, F. D. and L. A. Stange. 1965. Systematics and biological notes on the tribe Platymantispini (Neuroptera: Mantispidae) and the description of a new species of *Plega* from Mexico. *Canadian Entomologist* 97: 604–612.

Penny, N. D. 1982. Neuroptera of the Amazon Basin. Part 6. Mantispidae. *Acta Amazonica* 12: 415–463.

——— and C. A. da Costa. 1983. Mantispídeos do Brasil (Neuroptera: Mantispidae). *Acta Amazonica* 13: 601–687.

Sakagami, S. F., N. Gobbi, and R. Zucchi. 1990. Nesting biology of a quasisocial sphecid wasp *Trypoxylon fabricator*. *Japanese Journal of Entomology* 58: 846–862.

——— and R. Zucchi. 1978. Nests of *Hylaeus* (*Hylaeopsis*) *tricolor*: the first record of non-solitary life in colletid bees, with notes on communal and quasisocial colonies (Hymenoptera: Colletidae). *Journal of the Kansas Entomological Society* 51: 597–614.

Vesey-FitzGerald, D. F. 1936. Nesting habits of *Trypoxylon* (Hym. Sphec.) from Trinidad. *Proceedings of the Royal Entomological Society of London. Series A* 11: 111–115.

Urban, D. and J. S. Moure. 2007. *Hylaeini* Viereck, 1916. Pp. 710–722 *in:* Moure, J. S., D. Urban, and G. A. R. Melo eds. *Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region*. Sociedade Brasileira de Entomologia, Curitiba. xiv + 1058 pp.

Werner, F. G. and G. D. Butler, Jr. 1965. Some notes on the life history of *Plega banksi* (Neuroptera: Mantispidae). *Annals of the Entomological Society of America* 58: 66–68.

Woglum, R. S. 1935. *Symphrasis signata* Hagen. *Pan-Pacific Entomologist* 11: 119.